

NOTES ON *ACALYPHA* (EUPHORBIACEAE) IN
NORTH AMERICA

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ABSTRACT. Studies of three groups of North American *Acalypha* (Euphorbiaceae) species are presented. *Acalypha hederacea* and *A. monostachya* have traditionally been separated by plant sexuality and staminate inflorescence length, but examination of specimens from throughout the ranges of these two taxa show that they do not differ in either character. *Acalypha hederacea* should be treated as a synonym of *A. monostachya*. *Acalypha lindheimeri* and *A. phleoides* supposedly differ in tootching of the bracts subtending the pistillate flowers and in the shape of the leaf apices. However bract tootching is highly variable among these plants and leaf apex shape varies clinally, with numerous intermediates. *Acalypha lindheimeri*, based on specimens both geographically and morphologically extreme, should be treated as a synonym of *A. phleoides*. The *A. virginica* group has a complex taxonomic history. Taxonomic confusion has resulted from emphasis on characters that are unreliable because they show overlapping variation among the taxa. Five species can be distinguished based on unambiguous, nonoverlapping characters.

Key Words: *Acalypha*, *A. monostachya*, *A. phleoides*, *A. virginica*, Euphorbiaceae

In the course of my studies of *Acalypha* (Euphorbiaceae) for *Flora of North America* (Levin, in press), I have had to address several taxonomic problems in this large genus. Here I present the results of those investigations in more detail. There has not been a comprehensive study of the North American species of *Acalypha* published since Pax and Hoffman (1924) reviewed the entire genus. However, Miller (1964) studied the native species with varying depth and McVaugh (1961) studied two of the species that have distributions extending south into Mexico. In addition, the *A. virginica* group has received considerable attention (Cooperrider 1984; Reveal et al. 1990; Weatherby 1927, 1937, 1940).

ACALYPHA MONOSTACHYA CAV. AND *A. HEDERACEA* TORR.

Acalypha hederacea and *A. monostachya* have generally been distinguished by the length of the staminate spikes (Müller 1866;

Pax and Hoffmann 1924), with those of *A. hederacea* said to be about 6 cm long vs. 2–3 cm in *A. monostachya*. Plants assigned to both species are widespread in Mexico, but those in the United States have generally been called *A. hederacea*. McVaugh (1961) argued that the spikes of specimens generally called *A. hederacea* were rarely longer than 3 cm and often less than 2 cm, and therefore proposed that the taxa were not distinct. In contrast, Miller (1964) stated that the staminate spikes of *A. hederacea* averaged about 3.5 cm based on both measurements across the geographic range of the species and a population sample (presumably from Texas). Elsewhere Miller (1970) gave the length as 16–84 mm. She nowhere gave lengths for *A. monostachya*. Miller (1964) also argued that *A. hederacea* is mostly dioecious and generally has both terminal and axillary pistillate spikes, and implied that *A. monostachya* is monoecious and has strictly axillary pistillate spikes (both species, according to Miller and all other authors, have exclusively terminal staminate spikes). In the only other source of original observations, Johnston and Warnock (1962) studied *A. hederacea*. They gave the length of the staminate “thyrses”—presumably meaning the fertile portion of the inflorescence because they said the thyrses are peduncled—as “1–3 (–6) cm” and stated that the plants were usually monoecious. None of these authors studied type material of *A. monostachya*, although both McVaugh (1961) and Miller (1964) discussed Cavanilles’ (1800) illustration of this species. Miller (1964) apparently examined four of the seven syntypes of *A. hederacea*, but there is no indication McVaugh (1961) or Johnston and Warnock (1962) studied any of the type material.

Sexuality. I studied about 250 specimens from throughout the range of this complex from GH, LL, MICH, MO, NY, and TEX (herbarium abbreviations follow Holmgren et al. 1990). I observed three types of plants: pistillate flowers only, staminate flowers only, and monoecious (those with both staminate and pistillate flowers). Pistillate plants bore both axillary and terminal spikes, whereas staminate plants bore strictly terminal, long-pedunculate spikes. Inflorescence distribution on the monoecious plants was more complicated. Staminate flowers were always produced in terminal spikes. These were sometimes unisexual, but more often androgynous with one to three pistillate flowers near the base of the peduncle. On most monoecious plants the pistillate

spikes were all axillary, but some monoecious plants also bore terminal pistillate spikes.

I was able to locate five of the seven syntypes of *Acalypha hederacea*. Four of these (*Bigelow s.n.*, *Edwards & Eaton s.n.*, *Wright 648, 1814*) consist of unisexual plants, whereas *Wright 1813*, from Texas, is monoecious, with axillary pistillate spikes and terminal androgynous spikes bearing a single pistillate flower near the base of the peduncle of the otherwise staminate spikes. The type of *A. monostachya* was not designated, but apparently is *Née s.n.* (MA), the specimen itself from a plant cultivated at Madrid (R. McVaugh, pers. comm.). I haven't seen this specimen, but presumably it was the model for Cavanilles' (1800) illustration, which shows a monoecious plant with axillary pistillate inflorescences.

It is difficult to assess the sexuality of populations from herbarium specimens, because most collections consist of just a single plant. However it is still clear that within the *Acalypha hederacea/monostachya* complex, sexuality varies geographically. In the northern part of the range, both unisexual and monoecious plants are common, and from collections it appears that populations may consist of unisexual plants or may be mixed monoecious and pistillate. In only one case, *Marsh 3111* (TEX), from Coahuila, did I observe both staminate and monoecious plants in a single collection; this collection also included pistillate plants. Farther south, monoecious plants predominate and unisexual plants are almost absent. For example, of 55 specimens I observed from the Mexican states of Aguascalientes, Durango, Guanajuato, Hidalgo, Oaxaca, Puebla, Queretaro, San Luis Potosí, and Zacatecas, 51 were monoecious, two (one each from Guanajuato and Hidalgo) were pistillate, and two (one each from Durango and Hidalgo) were staminate.

To quantify this variation, I used the proportion of monoecious plants among all plants bearing staminate flowers, i.e., the sum of staminate plus monoecious plants. I used this statistic for two reasons. First, pistillate plants are likely to be over-represented in collections because the pistillate spikes persist longer than the staminate spikes. Second, as I discussed before, populations with monoecious plants may also contain pistillate plants, especially in the northern part of the range of the complex. Measured this way, Texas had the lowest frequency of monoecious plants, 56%. The northern tier of Mexican states (Chihuahua, Coahuila, Dur-

ango, Nuevo León, and Tamaulipas) had a higher rate of 80%, and the remaining eight Mexican states within the range had an overall rate of 98%, with many having no staminate plants at all. Although the frequency of monoecious plants clearly increases southwards (χ^2 test using the three geographic areas, $P < 0.0001$), monoecious plants are common throughout the range of the complex.

As might be expected because of the geographic pattern in sexuality and the historical identification of northern plants as *Acalypha hederacea* and southern plants as *A. monostachya*, there is a strong association between determination and sexuality (χ^2 test, $P < 0.0001$). About 68% of sampled plants historically determined as *A. hederacea* were monoecious, whereas 96% of *A. monostachya* were monoecious. Clearly, though, monoecy is common, even among plants that have been called *A. hederacea*. This result is consistent with McVaugh (1961) and Johnston and Warnock (1962), but not with Miller (1964, 1970).

Staminate spike length. I measured the staminate or androgynous spike length on the 191 specimens containing mature staminate or monoecious plants. Of these, 50 were determined as *Acalypha hederacea* and 141 as *A. monostachya*. The staminate and androgynous spikes consist of two portions, the peduncle and the fertile staminate portion, which I measured separately. To explore geographic variation, I divided the range into three regions, Texas, northern Mexico (Chihuahua, Coahuila, Durango, Nuevo León, and Tamaulipas), and central/southern Mexico (Aguascalientes, Guanajuato, Hidalgo, Oaxaca, Puebla, San Luis Potosí, and Zacatecas), and randomly sampled 48 specimens from each (48 was chosen because that was the number of specimens available from the third region). Peduncle length, staminate portion length, and total spike length did not significantly differ among the three areas (Table 1).

I also tested for differences between monoecious and staminate plants, and between plants historically determined as *A. hederacea* and *A. monostachya*, using all 191 specimens. Lengths of the peduncle, staminate portion, and total spike did not significantly differ by plant sexuality (Table 2A) or by historical determination (Table 2B). Among all the specimens, the length of the fertile portion of the staminate spike was 1–4 cm (mean = 2.1 cm) and the total length of the spike was 1.9–7.9 cm (mean = 4.0 cm).

Table 1. Regional variation in staminate and androgynous inflorescence dimensions that have been used to distinguish *Acalypha hederacea* and *A. monostachya*. Regions are A: Texas, B: northern Mexico (Chihuahua, Coahuila, Durango, Nuevo León, and Tamaulipas), and C: central and southern Mexico (Aguascalientes, Guanajuato, Hidalgo, Oaxaca, Puebla, Queretaro, San Luis Potosí, and Zacatecas). Lengths are shown as mean \pm standard error based on 48 herbarium specimens from each region. Probabilities are for the given *F* values obtained by one-way analysis of variance.

	Region			<i>F</i>	<i>P</i>
	A	B	C		
Peduncle length (cm)	1.84 \pm 0.073	1.98 \pm 0.084	2.03 \pm 0.103	1.305	0.274
Staminate portion length (cm)	2.08 \pm 0.083	2.10 \pm 0.084	2.22 \pm 0.096	0.745	0.477
Total inflorescence length (cm)	3.92 \pm 0.140	4.04 \pm 0.153	4.25 \pm 0.177	1.134	0.325

Table 2. Comparison of staminate and androgynous inflorescence dimensions that have been used to distinguish *Acalypha hederacea* and *A. monostachya*. Herbarium specimens are classified according to (A) sexuality (unisexual plants vs. monoecious) and (B) original determination (*A. hederacea* vs. *A. monostachya*). Lengths are shown as mean \pm standard error. Probabilities are based on two-tailed *t*-tests assuming unequal sample variances.

A. Plant Sexuality				
	Unisexual Plants (n = 47)	Monoecious (n = 144)	<i>t</i>	<i>P</i>
Peduncle length (cm)	1.85 \pm 0.065	1.95 \pm 0.051	1.176	0.242
Staminate portion length (cm)	2.06 \pm 0.085	2.14 \pm 0.053	0.845	0.400
Total inflorescence length (cm)	3.91 \pm 0.133	4.10 \pm 0.093	1.122	0.265
B. Original Determination				
	<i>A. hederacea</i> (n = 141)	<i>A. monostachya</i> (n = 50)	<i>t</i>	<i>P</i>
Peduncle length (cm)	1.89 \pm 0.046	2.04 \pm 0.092	1.522	0.132
Staminate portion length (cm)	2.12 \pm 0.052	2.14 \pm 0.093	0.235	0.815
Total inflorescence length (cm)	4.00 \pm 0.088	4.18 \pm 0.163	0.979	0.330

These results do not support the use of staminate spike length to distinguish *Acalypha hederacea* and *A. monostachya*. It is possible that the complex has two species, differing in sexuality, with broadly overlapping geographic ranges. However, I found no other morphological features that differentiate two groups. I suspect that Miller (1964) studied relatively few specimens (she gave no sample size) and that she measured the entire staminate spike, whereas McVaugh (1961) measured only the fertile staminate portion, hence the differences in their observations. When interpreted this way, their measurements are consistent with mine. Because I can find no way to distinguish two species, I agree with McVaugh (1961) that only a single species is involved, which should be called *A. monostachya*.

ACALYPHA PHLEOIDES CAV. AND *A. LINDHEIMERI* MÜLL. ARG.

Acalypha phleoides is traditionally interpreted as a species of the arid highlands of eastern and central Mexico, ranging as far

north as Chihuahua and Coahuila. Overlapping with this in northern Mexico and extending into Arizona, New Mexico, and Texas, is what is usually called *A. lindheimeri*. According to Müller (1866), *A. lindheimeri* has acuminate rather than acute leaves, the terminal tooth of the bracts subtending the pistillate flowers prolonged rather than equal to the other teeth, and more slender style branches.

I examined more than 400 specimens from throughout the range of these two taxa. Leaves on plants from Texas are mostly rhombic-ovate and acuminate, though lower leaves tend to be broader relative to their length and have acute apices. Sometimes the bracts subtending the pistillate flowers have elongate terminal teeth, as they do on two of the isosyntypes of *Acalypha lindheimeri* I have seen (*Lindheimer 520* [CAN!, GH!, MO!] and *Lindheimer 688* [GH!, MO!]), but more often all the teeth are subequal, as they are on the third isosyntytype I examined (*Wright 1815* [GH!]). Leaves of plants from central Mexico south are ovate to suborbicular (especially the lower leaves) with consistently acute apices. The teeth of the bracts subtending the pistillate flowers are consistently subequal. There is also a tendency for the more southerly plants to have denser and coarser pubescence than the more northerly plants, especially those from Texas. Plants from Arizona, e.g., *Blumer 1498* (ARIZ!, GH!, ISC!, NMC!; the type of *A. lindheimeri* var. *major* Pax & K. Hoffm.), and northern Mexico are intermediate between the Texan and central Mexican plants, with no obvious discontinuities. I could distinguish no differences in style branch thickness. The difficulty of quantifying leaf shape and its variation within individual plants makes statistic analysis extremely problematic. However, because leaf shape varies apparently continuously throughout the range of the group and bract tooting shows no consistent pattern, it appears that *A. lindheimeri* was based on a few extreme specimens of *A. phleoides*. It therefore seems preferable to treat all these plants as a single species using the older name, *A. phleoides*.

ACALYPHA VIRGINICA GROUP

The *Acalypha virginica* group has received the greatest study of any North American members of the genus. Through much of the 18th and 19th centuries, there was considerable disagreement in interpretation of this group, but most authors recognized either

one or two taxa. Müller (1865, 1866), however, recognized four taxa in the group, all as varieties of *A. virginica*. In a series of papers, Weatherby (1927, 1937, 1940) attempted to sort out the variation in the group and to resolve a nagging typification problem surrounding the name *A. virginica*. Ultimately he recognized three species, *A. gracilens* A. Gray with three varieties [var. *gracilens*, var. *fraseri* (Müll. Arg.) Weath., and var. *monococca* Engelm. ex A. Gray], *A. rhomboidea* Raf. with two varieties [var. *rhomboidea* and the newly described var. *deamii* (Weath.) Weath.], and *A. virginica*. Unfortunately, the typification problem was not finally resolved until 1990 (Reveal et al. 1990), when conservation of the name and type of *A. virginica* established Weatherby's (1937) treatment.

Weatherby's treatment (1937) continues to be widely used today. However, two additional treatments have also had some influence. First, Miller (1964, 1969, 1970; Gandhi and Hatch 1988) recognized five species in the group, *Acalypha deamii* (Weath.) H. E. Ahles, *A. gracilens*, *A. monococca* (Engelm. ex A. Gray) Lill. W. Miller & Gandhi, *A. rhomboidea*, and *A. virginica*. In addition to segregating *A. monococca* as a separate species, she further realigned *A. gracilens* by treating var. *fraseri* as a synonym of *A. gracilens* var. *gracilens* and recognizing *A. gracilens* var. *delzii* Lill. W. Miller. The second treatment was by Cooperrider (1984, 1995). Studying almost exclusively plants from Ohio and therefore not considering *A. gracilens* or *A. monococca*, he treated the remaining three taxa as varieties of *A. virginica* [thus *A. virginica* var. *deamii* Weath., *A. virginica* var. *rhomboidea* (Raf.) Cooperr., and *A. virginica* var. *virginica*].

In justifying his treatment, Cooperrider (1984) stated that he saw many intermediates between his varieties of *Acalypha virginica*, particularly between var. *rhomboidea* and var. *virginica*, and further that "no single reliable diagnostic character or combination of characters" separates these taxa. Based on my observations, I disagree. Instead, the apparent intergradation and lack of diagnostic characters reflect two problems. First, most of the characters used by Weatherby (1927, 1937) and Miller (1964, 1970) are not always reliable. Second, and clearly related to the first, misidentifications are rife in herbaria. On the approximately 4,000 specimens of *A. rhomboidea* and *A. virginica* I examined, about 18% of the annotations applied since 1940 (sufficiently after Weatherby's publications to allow them to become widely

used) were misidentified, about half of these bearing names of the other taxon. (In this calculation I excluded Miller's annotations, with which I almost entirely concur.) Cooperrider's own identifications are instructive. I have seen 96 specimens of the two species he annotated. We agree on almost all that he called *A. virginica* var. *rhomboidea*, but we would agree on only 44% (eight of 18) that he called *A. virginica* var. *virginica*. Perhaps this high frequency of misidentifications prevented him from seeing the clear and reliable distinctions between these taxa. I found a similar rate of misidentifications among specimens of *A. gracilens* and *A. virginica*. (Another consequence of the high rate of misidentifications is that most published range maps are not reliable.)

Most regional floras that treat several taxa in the *Acalypha virginica* group (e.g., Cooperrider 1995; Gleason and Cronquist 1991; Miller 1970; Mohlenbrock 1982, 1986; Radford et al. 1968; Steyermark 1963) distinguish them using some combination of stem pubescence (long spreading and short incurved vs. just short incurved), petiole length (either absolute or relative to leaf length), leaf shape, shape and number of teeth or lobes on the bracts subtending the pistillate flowers, pubescence on these bracts, carpel number, and seed size. Table 3 summarizes these characteristics for the five species recognized by Miller (1964, 1970) and me. Some of these characters are unambiguous and serve to distinguish individual taxa. For example, *A. virginica* is unique in having long spreading eglandular trichomes on the abaxial surface of the pistillate bracts, and mature plants always bear these (the lowermost bracts on the plant may lack the spreading hairs, however). Similarly, *A. deamii* always has gynoecia with two carpels and *A. monococca* has gynoecia with one carpel, whereas the remaining species have three carpels. Also *A. deamii* has seeds that are at least 2.2 mm long, whereas the other species have seeds no more than 2.0 mm long, with the exception of *A. monococca*, which occasionally has seeds to 2.4 mm long. Outgroup comparison with *A. alopecuroides* Jacq., *A. arvensis* Poepp., *A. australis* L., *A. brachystachya* Hornem., *A. indica* L., and *A. mexicana* Müll. Arg. suggests that these unique characteristics are all apomorphies of the individual species (Table 3).

Other characters may be useful in separating otherwise similar species. A sample of 100 specimens each of *Acalypha virginica* and *A. rhomboidea* showed that the number of lobes on the pis-

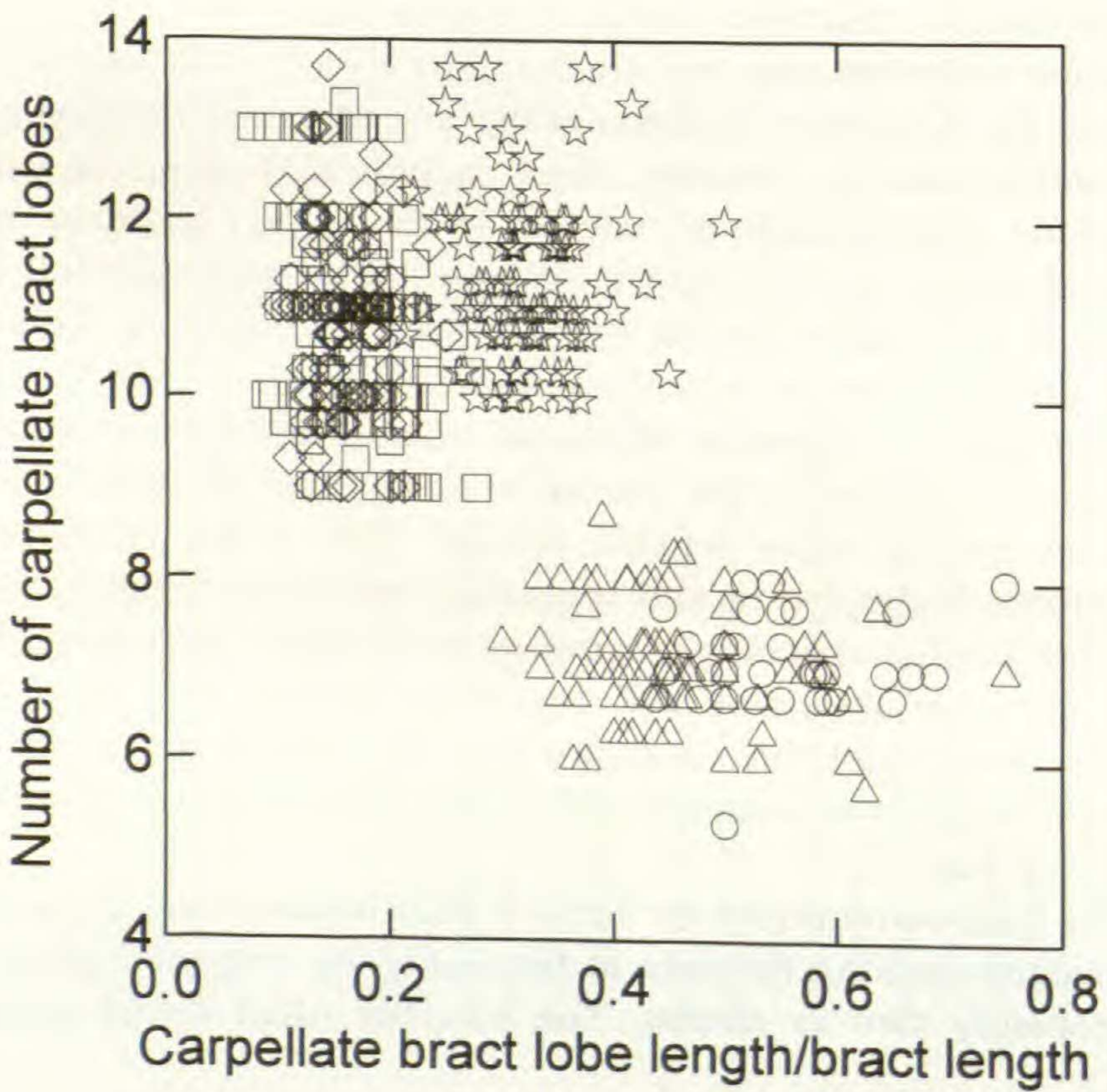
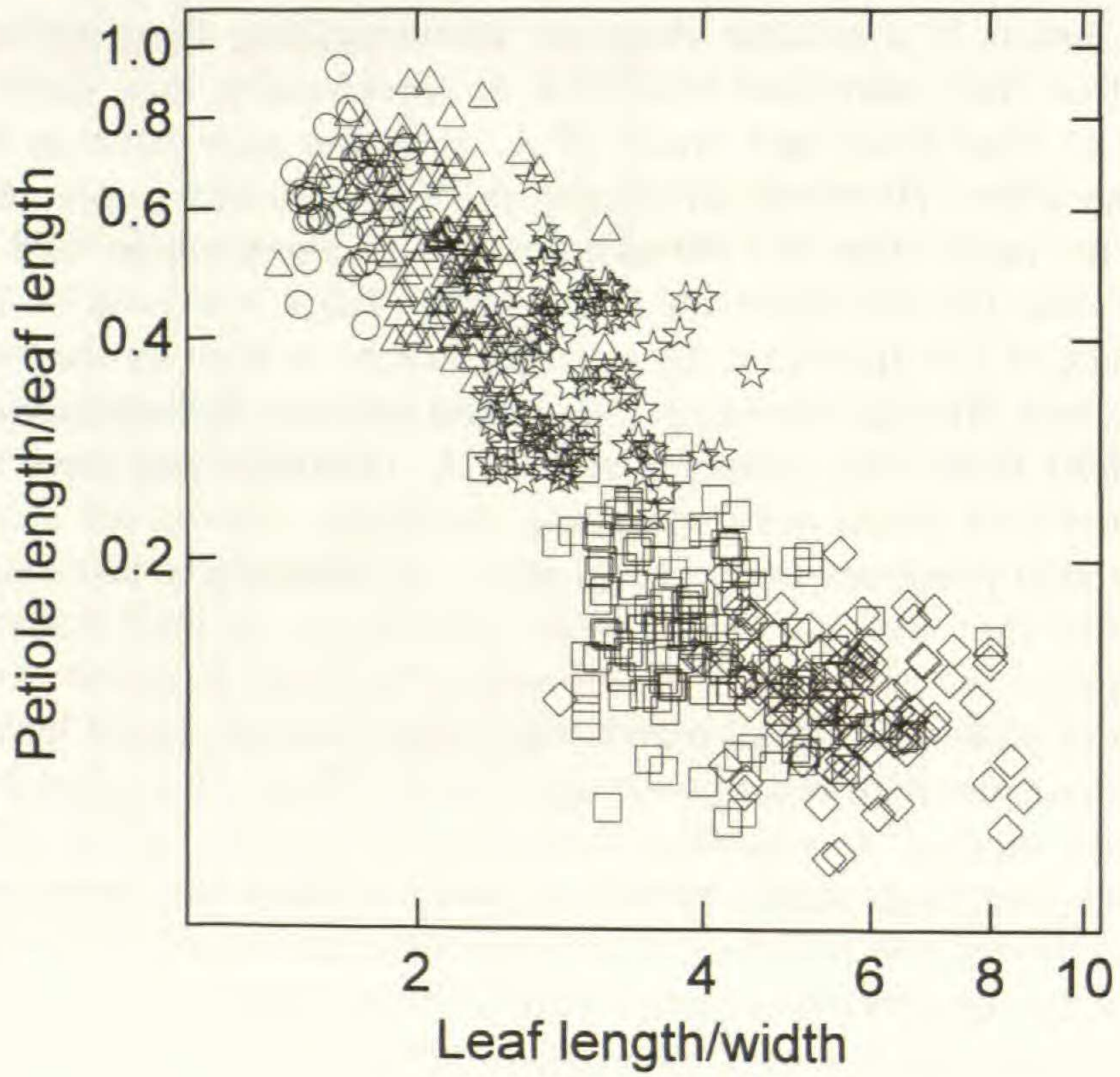
Table 3. Summary of characters often used to separate species in the *Acalypha virginica* group, compiled from herbarium specimens from throughout the geographic ranges of the species. Values for quantitative characters are ranges. Sample sizes are $n = 100$ except for *A. deamii*, a rare species for which $n = 35$. Asterisks (*) indicate unambiguous unique species-level apomorphies based on outgroup comparison with *A. alopecuroides*, *A. arvensis*, *A. australis*, *A. brachystachya*, *A. indica*, and *A. mexicana*.

Character	<i>A. deamii</i>	<i>A. gracilens</i>	<i>A. mono-</i> <i>cocca</i>	<i>A. rhomboidea</i>	<i>A. virginica</i>
Stems with long spreading hairs	Never	Never	Never	About 5% of plants	About 90% of plants
Petiole length (cm)	2.5–7.0	0.2–1.4	0.2–0.9	0.8–7.0	0.7–3.6
Petiole length/leaf blade length	0.42–0.94	0.09–0.30	0.08–0.20	0.34–0.89	0.23–0.66
Leaf blade length/width	1.5–2.0	2.3–8.0	2.8–8.7	1.4–3.2	2.1–4.5
Pistillate bracts with long spreading eglandular hairs	No	No	No	No	Yes (except sometimes the lowermost on the plant)*
Pistillate bracts with red glands	No	Yes	Yes	No	No
Pistillate bract tooth (lobe) length (mm)	4.5–9.0	0.6–2.2	0.9–2.2	1.8–9.0	1.6–5.0
Pistillate bract tooth (lobe) length/pistillate bract length	0.44–0.75	0.08–0.28	0.10–0.25	0.30–0.75	0.21–0.50
Number of teeth/lobes on pistillate bracts (average of 3–5 bracts)	5.3–8.0	9.0–13.3	9.0–13.7	5.7–8.7	10.0–13.7
Carpel number	2*	3	1*	3	3
Seed length (mm)	2.2–3.1*	1.1–1.9	1.6–2.4	1.3–2.0	1.3–1.8

tillate bracts is a reliable character distinguishing these species. It is true that individual bracts of *A. rhomboidea* may have as many as nine lobes and bracts of *A. virginica* may have as few as nine lobes. However, averaging three to five bracts per plant gave no more than 8.7 lobes/bract for *A. rhomboidea* and no fewer than 10 lobes/bract for *A. virginica* (Table 3; Figure 1). The presence of red glands on the pistillate bracts, at least on the tooth apices and often scattered on the abaxial surface, distinguishes *A. gracilens* from very young plants of *A. virginica* that have not yet produced bracts with spreading trichomes. (*Acalypha monococca* also produces these red glands.) A particularly interesting situation that has not been noted previously is that scattered throughout the range of *A. rhomboidea*, but more frequent in the southern states, are small plants with short petioles, small leaves, and small pistillate bracts with short teeth. These often appear in herbaria labeled *A. gracilens*, presumably because of the short petioles and bract teeth. However, tooth number is consistently nine or fewer, the petioles are at least 40% the length of the leaf blades, the bract teeth are more than 30% the length of the bracts, and the bracts do not bear red glands. These characteristics clearly demonstrate that these plants are simply small *A. rhomboidea* rather than *A. gracilens* (Table 3; Figure 1).

Some characteristics that are frequently used to distinguish species in the *Acalypha virginica* group are not consistent and overlap among species. Notably, these include leaf shape (described by blade length/width; all species in this group have the same general shape, so this ratio is an appropriate statistic) and both absolute and relative petiole lengths (Table 3; Figure 1). Although very different species may show no overlap, others, like *A. rhomboidea* and *A. virginica*, show no reliable differences in these characters. Neither is the presence or absence of spreading trichomes on the stems reliable. Nearly 10% of the *A. virginica* specimens I sampled lacked spreading trichomes, whereas 5% of *A. rhomboidea* specimens sampled bore them. Spreading stem trichomes are absent on the remaining species. It is likely that use of these unreliable characteristics has contributed to the relatively frequent misidentifications and the taxonomic confusion in this group.

The data summarized in Table 3 demonstrate that, in fact, intermediates among the taxa in the *Acalypha virginica* group are exceedingly rare or absent. The taxa are often found growing



nearby or together, notably *A. deamii* with *A. rhomboidea*; *A. gracilens* with *A. monococca*, *A. rhomboidea*, or *A. virginica*; *A. monococca* with *A. virginica*; and, most frequently, *A. rhomboidea* with *A. virginica* (pers. obs.). Yet examination of over 6500 specimens revealed no clear evidence for hybridization, nor have I found evidence for hybridization during field work throughout much of the range of these taxa.

The presence of unique apomorphies (Table 3) for *Acalypha deamii* (two carpels/flower, seeds at least 2.2 mm long), *A. monococca* (one carpel/flower), and *A. virginica* (long spreading eglandular trichomes on the abaxial surface of the pistillate bracts), supports recognition of these taxa as species under both the phylogenetic (Davis and Nixon 1992; Nixon and Wheeler 1990) and genealogical (Baum and Donoghue 1995; de Queiroz and Donoghue 1988; Olmstead 1995) species concepts. Because they are distinguishable by nonoverlapping characters, *A. gracilens* and *A. rhomboidea* would also be species under the phylogenetic species concept, but because they lack unique apomorphies (insofar as known), they would be metaspecies under the genealogical species concept. In either case, under both of these cladistically based species concepts, all the taxa in the *A. virginica* group should be recognized at the rank of species. I do not recognize any infraspecific taxa in *A. gracilens* because variation in this species is clinal over broad geographic areas (Levin 1998).

Key to the species of the *Acalypha virginica* group. I also include in the key the introduced *Acalypha australis*, which may be confused with members of this group.

1. Leaf blades linear to oblong-lanceolate; petioles rarely more than $\frac{1}{4}$ the length of the leaf blades; bracts of pistillate flowers with deltoid teeth $\frac{1}{10}$ – $\frac{1}{4}$ length of the bract, with sparse to dense sessile red glands (2)

←

Figure 1. Plots showing the variation in the *Acalypha virginica* group along four characters. All species are represented by $n = 100$ except *A. deamii*, a rare species with $n = 35$. Note that both axes in the upper graph are logarithmic. Key to symbols: *A. deamii* ○, *A. gracilens* □, *A. monococca* ◇, *A. rhomboidea* △, and *A. virginica* ☆.

2. Pistil with 3 carpels, usually producing 3 seeds
 *Acalypha gracilens*
2. Pistil with 1 carpel, producing 1 seed
 *Acalypha monococca*
1. Leaf blades broadly lanceolate to ovate; petioles more than $\frac{1}{4}$
 (usually more than $\frac{1}{3}$) the length of the leaf blades; bracts
 of pistillate flowers either with triangular to lanceolate
 lobes more than $\frac{1}{4}$ the length of the bract or with rounded
 teeth less than $\frac{1}{10}$ the length of the bract, lacking red
 glands (3)
3. Bracts of pistillate flowers hirsute with dense long
 spreading non-glandular hairs (also ciliate and often
 with stalked glands), and with (9-) 10-14 (-16)
 lobes more than $\frac{1}{4}$ the length of the bract; stems
 usually hirsute with long spreading hairs
 *Acalypha virginica*
3. Bracts of pistillate flowers without long spreading non-
 glandular hairs (may be ciliate or with stalked
 glands), and with either (5-) 7-9 (-11) lobes more
 than $\frac{1}{3}$ the length of the bract or 12-15 teeth less
 than $\frac{1}{10}$ the length of the bract; stems very rarely
 hirsute (4)
4. Bracts of pistillate flowers with 12-15 rounded teeth
 less than $\frac{1}{10}$ the length of the bract
 *Acalypha australis*
4. Bracts of pistillate flowers with (5-) 7-9 (-11) lan-
 ceolate lobes more than $\frac{1}{3}$ the length of the bract
 (5)
5. Pistils with 3 carpels; seeds <2.1 mm long
 *Acalypha rhomboidea*
5. Pistils with 2 carpels; seeds >2.1 mm long
 *Acalypha deamii*

Taxonomic treatment of the *Acalypha virginica* group.

1. ***Acalypha deamii*** (Weath.) H. E. Ahles in Jones & Fuller, Vasc.
 Pl. Illinois 301. 1955.

Acalypha virginica L. var. *deamii* Weath., Rhodora 29: 197. 1927. TYPE:
 UNITED STATES. Indiana: Dearborn Co., road along White Water
 River, 2 mi. northeast of Logan, Oct 20, 1924. C.C. Deam 41107

(HOLOTYPE: IND!; ISOTYPE: GH!). *Acalypha rhomboidea* Raf. var. *deamii* (Weath.) Weath., *Rhodora* 39: 16. 1937.

2. ***Acalypha gracilens*** A. Gray, *Manual* 408. 1848. TYPE: UNITED STATES. Virginia. *F.I.X. Rugel s.n.* (LECTOTYPE—designated by G. A. Levin, *Syst. Bot.* 23:285. 1998[1999]: GH!; ISOLECTOTYPE: G). *Acalypha virginica* L. var. *gracilens* (A. Gray) Müll. Arg., *Linnaea* 34: 45. 1865.

Acalypha virginica L. var. *fraseri* Müll. Arg., *Linnaea* 34: 45. 1865. TYPE: UNITED STATES. South Carolina. *J. Fraser s.n.* (HOLOTYPE: G-DC, microfiche!). *Acalypha gracilens* A. Gray var. *fraseri* (Müll. Arg.) Weath., *Rhodora* 29: 202. 1927.

Acalypha gracilens A. Gray var. *delzii* Lill. W. Miller, *Sida* 3: 447. 1969. TYPE: UNITED STATES. Arkansas: Hot Spring Co., Bismarck P.O., Jul 14, 1957. *D. Demaree 39432* (HOLOTYPE: SMU!; ISOTYPES: GH!, KANU!, OKL!).

3. ***Acalypha monococca*** (Engelm. ex A. Gray) Lill. W. Miller & Gandhi, *Sida* 13: 123. 1988.

Acalypha gracilens A. Gray var. *monococca* Engelm. ex A. Gray, *Manual*, ed. 2, 390. 1856. TYPE: UNITED STATES. Missouri: St. Louis Co., limestone precipices on the banks of the Mississippi River near St. Louis, Sep–Oct 1844. *G. Engelmann s.n.* (HOLOTYPE: GH!; ISOTYPE: WIS!). *Acalypha gracilens* A. Gray ssp. *monococca* (Engelm. ex A. Gray) G. L. Webster, *J. Arnold Arbor.* 48: 373. 1967.

4. ***Acalypha rhomboidea*** Raf., *New Fl.* 1: 45. 1836. TYPE: UNITED STATES. South Carolina. *C.S. Rafinesque s.n.* (LECTOTYPE—designated by C. A. Weatherby, *Rhodora* 42: 96. 1940: G-DEL, photo at GH!). *Acalypha virginica* L. var. *genuina* Müll. Arg., *Linnaea* 34: 44. 1865. *Acalypha virginica* L. var. *rhomboidea* (Raf.) Cooperr., *Michigan Bot.* 23: 165. 1984.

5. ***Acalypha virginica*** L., *Sp. Pl.* 1003. 1753. TYPE (conserved): UNITED STATES. Virginia. *J. Clayton 201* (HOLOTYPE: BM, drawing at GH!). *Acalypha virginica* L. var. *intermedia* Müll. Arg., *Linnaea* 34: 45. 1865.

Acalypha digyneia Raf., *Fl. Ludov.* 112. 1817. TYPE: none located.

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LITERATURE CITED

- BAUM, D. A. AND M. J. DONOGHUE. 1995. Choosing among alternative "phylogenetic species" concepts. *Syst. Bot.* 20: 560–573.
- CAVANILLES, A. J. 1800. Descripcion del genero Bonplandia, y de otras plantas. *Anales Hist. Nat. Madrid* 2: 12–142.
- COOPERRIDER, T. S. 1984. Some species mergers and new combinations in the Ohio flora. *Michigan Bot.* 23: 165–168.
- . 1995. The Dicotyledoneae of Ohio. Part 2. Linaceae Through Campanulaceae. Ohio State Univ. Press, Columbus, OH.
- DAVIS, J. I. AND K. C. NIXON. 1992. Populations, genetic variation, and the delimitation of phylogenetic species. *Syst. Biol.* 41: 421–435.
- DE QUEIROZ, K. AND M. J. DONOGHUE. 1988. Phylogenetic systematics and the species problem. *Cladistics* 4: 317–338.
- GANDHI, K. N. AND S. L. HATCH. 1988. Nomenclatural changes in *Acalypha* (Euphorbiaceae) and *Chamaecrista* (Fabaceae). *Sida* 13: 122–123.
- GLEASON, H. A. AND A. CRONQUIST. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. The New York Botanical Garden, Bronx, NY.
- HOLMGREN, P. K., N. H. HOLMGREN, AND L. C. BARNETT, eds. 1990. *Index Herbariorum. Part I: The Herbaria of the World*, 8th ed. The New York Botanical Garden, Bronx, NY.
- JOHNSTON, M. C. AND B. H. WARNOCK. 1962. The four species of *Acalypha* (Euphorbiaceae) in far western Texas. *SouthW. Naturalist* 7: 182–190.
- LEVIN, G. A. 1998 [1999]. Evolution in the *Acalypha gracilens/monococca* complex (Euphorbiaceae): Morphological analysis. *Syst. Bot.* 23: 269–288.
- . In press. *Acalypha* (Euphorbiaceae). In: *Flora of North America* Editorial Committee, eds. 1993+. *Flora of North America North of Mexico*, Vol. 12. Oxford Univ. Press, New York and Oxford.
- MCVAUGH, R. 1961. Euphorbiaceae novae Novo-Galicianae. *Brittonia* 13: 145–205.
- MILLER, L. W. 1964. A taxonomic treatment of the species of *Acalypha* in the United States. Ph.D. dissertation, Purdue University, West Lafayette, IN.
- . 1969. *Acalypha gracilens* Gray var. *delzii* L. Miller, var. nov. *Sida* 3: 447.
- . 1970. *Acalypha*, pp. 943–947. In: D. S. Correll and M. C. Johnston,

- eds., Manual of the Vascular Plants of Texas. Texas Research Foundation, Renner, TX.
- MOHLENBROCK, R. H. 1982. Flowering Plants: Basswoods to Spurges. Southern Illinois Univ. Press, Carbondale, IL.
- . 1986. Guide to the Vascular Flora of Illinois, revised and enlarged ed. Southern Illinois Univ. Press, Carbondale, IL.
- MÜLLER, J. 1865. Vorläufige Mitteilungen aus dem für De Candolle's Prodrum bestimmten Manuscript. *Linnaea* 34: 1–126.
- . 1866. Euphorbiaceae, pp. 189–1286. *In*: A. De Candolle, ed., *Prodrum Systematis Naturalis Regni Vegetabilis*, Vol. 15(2). Victor Masson, Paris.
- NIXON, K. C. AND Q. D. WHEELER. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6: 211–223.
- OLMSTEAD, R. G. 1995. Species concepts and plesiomorphic species. *Syst. Bot.* 20: 623–630.
- PAX, F. AND K. HOFFMANN. 1924. Euphorbiaceae–Crotonoideae–Acalypheae–Acalyphinae, *Additamentum VII*, pp. 1–231. *In*: A. Engler, ed., *Das Pflanzenreich*, IV, 147. XVI (Heft 85).
- RADFORD, A. E., H. A. AHLES, AND C. R. BELL. 1968. Manual of the Vascular Flora of the Carolinas. Univ. of North Carolina Press, Chapel Hill, NC.
- REVEAL, J. L., C. E. JARVIS, AND F. R. BARRIE. 1990. Proposal to conserve the name and type of *Acalypha virginica* L. (Euphorbiaceae). *Taxon* 39: 361–363.
- STEYERMARK, J. A. 1963. Flora of Missouri. Iowa State Univ. Press, Ames, IA.
- WEATHERBY, C. A. 1927. The group of *Acalypha virginica* in eastern North America. *Rhodora* 29: 193–204.
- . 1937. The typification of *Acalypha virginica* L. *Rhodora* 39: 14–16.
- . 1940. Rafinesque types in the group of *Acalypha virginica*. *Rhodora* 42: 96.